Moult Increments and Frequency in the Freshwater Crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney Region, Australia

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Euastacus spinifer mark-recapture data have been used to investigate relationships of moulting frequency and moult increments to biological or environmental factors. Small individuals (20–35mm CL) usually moult three times per year (total frequency range 1–6); the medium size class (35–55mm CL) typically moults twice (total frequency range 1–3); large specimens (>55mm CL) moult once per year. No differences have been detected in annual frequencies related to sex or site and it is suggested that moulting is independent of sex and state of maturity.

Moulting seasons for small and medium *E. spinifer* of both sexes are similar but trends for large females and males differ. Moulting activity in the small class commences in September or October and declines in April or May; the medium size class exhibits two periods of activity (October-November, February-May). Large females moult from March to June (with a peak of activity in May); large males moult from November to January. Temperature appears to be the prime environmental regulator of growth and moulting activity at all sizes usually only occurs when water temperatures exceed 14–15°C.

No significant differences in moult increment have been detected between immature females, normal males or precocious males nor have any differences been found between season or location. Increments of mature females are smaller than males of comparable size and reproduction is considered to decrease increment size in females but not in males. Considerable increment variation, at both individual and populational levels, was detected. Food availability and population density are suggested as factors contributing to this variation. Analyses demonstrated an increase in moult increment with rising pre-moult carapace length in the range of 20–55mm, but above this size increments become constant.

INTRODUCTION

Overall growth in crustaceans is the result of two fundamental components; these are the amount by which an individual increases in size at moulting (i.e., moult increment) and moult frequency (Hartnoll 1983). Variation in growth rate may result from variation in either or both of these components. So in this study, as in others (Bennett 1974; Berry 1971; Kurata 1962; Mauchline 1977), the contributions of moult increment and moult frequency have been analysed separately.

A systematic approach was developed to extract maximum information from mark-recapture data, based on Hepper (1967), Mauchline (1977) and Underwood (1975). Development of this approach involved extensive preliminary analyses, using sub-sets of

Euastacus spinifer data, to assess contributions of different factors to observed variation (Turvey 1980). Early in the study it became clear that information on moult frequency was essential for the interpretation of temporal variations in moult increment, so it is treated first. The time of year during which moulting occurred was also of interest, as it may have reflected the effects of environmental factors on growth, or changes in growth patterns of individuals at different stages of the life cycle. Investigations of moult increment involved a survey to identify the factors that might have affected the growth of individual *E. spinifer*, as preliminary examination of data indicated that moult increments were highly variable for specimens of any given size.

With the notable exception of studies on *E. bispinosus* (Honan and Mitchell 1995) there are no published studies of moult frequency or growth increments in members of the genus *Euastacus*. Objectives of this paper are: to investigate variation in both frequency and seasonality of moulting with respect to sex, size and capture site; to relate the observed moult seasonality to changes in water temperature; to determine if size-independent variation in moult increment is related to sex, season or site; to assess if increment variation resulted from individual variability, effects of pre-moult carapace length, measurement error or other factors; to interpret variation in moult increment with size based on the analyses for size-independent variation.

MATERIALS AND METHODS

The frequency analyses are based on the mark-recapture sampling conducted in Pools 3 and 7 at the study site during the period May 1977 to December 1978. The site and sampling techniques were documented in Turvey and Merrick (1997a,b). Moult stage notation was based on Passano (1960).

Annual Moult Frequency

Total annual growth for individuals 20–55mm CL was estimated as the difference between carapace length measurements of marked individuals taken 12 months apart. These annual growth increments were subdivided into a series of likely moult increments based on the results of Turvey (1980), and the number of moults per year was determined for each cray as the number of consecutive increments.

Where annual growth could not be divided into consecutive moult increments, the contributing number of moults was estimated as follows. Average moult increments were determined for 5mm size classes, commencing at 19.95mm CL, separately for each sex and location. For each individual, the average moult increment (of relevant size class) was added to the length initially recorded to provide a new CL; this process was repeated. until the annual moult frequency could be estimated as the number of average increments providing the final CL closest to that recorded at the end of twelve months.

Annual moult frequencies of individuals exceeding 55mm CL were determined from numbers of consecutive moult increments over periods of 12–15 months. Annual frequencies of all samples were plotted against initial CL. For analysis, the total CL range was divided into three intervals (20–35mm, 35–55mm, and 55–100mm) designated as small, medium and large respectively.

Seasonality in Moulting

Separate criteria were used to determine the commencement and termination of periods of concentrated moulting activity. Initiation of moulting was determined as follows. Captured individuals were classified into moult stages Ce (early intermoult) or C

(intermoult) at each monthly sampling of the mark-recapture study (Turvey and Merrick 1997b); percentages of specimens in each catch that were in moult stage Ce indicated the level of recent moult activity. These values (referred to as percentages of post-moult crayfishes) were calculated separately for small, medium and large individuals of each sex, from each of the two pools. These calculations were plotted against month of sampling. The onset of moulting activity was considered to occur during the month in which the post-moult percentage increased markedly from a previously low value.

Decline in moulting activity was determined in the following way. Using mark-recapture records and supplementary analyses (Turvey 1980) it was possible to determine whether a crayfish had moulted during the period between any two captures, if the interval was two months or more. So a substantial increase in the percentage that definitely did not moult, in any given month, was used to indicate decreasing moult activity. This value (referred to as the percentage of non-moulting crayfishes) was calculated for the same groups as those for which post-moult percentages had been determined.

Moulting Activity and Water Temperature

Moulting in small *E. spinifer* was compared directly with the thermal cycle. Water temperatures recorded at each sampling were plotted on an annual time scale and months during which each moulting season commenced or ceased were also marked.

Moult Increment and Sex, Season or Site

Increments were tabulated separately for males and females from the two pools. These data were further subdivided into classes, based on individual pre-moult CL, for each of several seasons of moulting activity.

Increments of small individuals (20–35mm CL) were compared for the periods May–October 1977, October 1977–February 1978, February–August 1978 and May–October 1978. Moult increments of medium *E. spinifer* (35–55mm CL) were compared for the periods May–November 1977, December 1977–August 1978 and May–November 1978.

The moult increments of these small and medium classes were compared by calculating the linear regressions of increment on pre-moult CL and comparing slopes as well as elevations of the lines using analysis of covariance (Snedecor and Cochran 1967). Where slopes were not significantly different, the differentials between elevations were used to indicate differences in average moult increment. A Student Newman Keuls test (Zar 1974) was used to test for significant differences among elevations.

Initial comparisons were made between the sexes at each season and location. Where regressions for the sexes were not significantly different ($p > 0.05$), data for both sexes were combined and compared between seasons, separately for each location. Where seasonal regressions were not significantly different ($p > 0.05$), data for similar seasons were combined and regressions for the sets of similar seasons were compared between locations. When there were no significant differences between slopes or elevations for a number of groups, the regression line for the combined data has been presented. Where elevations differed significantly but slopes did not, regressions with the pooled slope for all groups (Snedecor and Cochran 1967) have been plotted through the means of each different group.

Seasonal comparisons were not conducted for large individuals (exceeding 55mm CL); comparisons between males and females of 55–70mm CL were treated in the manner described for smaller individuals. Males considered in all the above comparisons were of the normal type, but comparisons were also made between increments of precocious (very small, sexually mature) males, normal males and females (for the size range 20–25mm CL) during the period October 1977 to February 1978 in Pool 3. Where data

were inadequate to allow comparison between sexes for a season, combined data were used for comparison between seasons.

Moult Increment Variation and Other Factors

Mark-capture records were examined for instances where moult increments had been recorded in consecutive seasons for an individual. Data were arranged into classes based on initial CL, location of capture and the two seasons involved. Multiple regressions of moult increment for the second season (Y) on pre-moult CL for the second season (X_1) and increment for the first season (X_2) were calculated for each class. Any correlation between moult increment and previous increment would include an estimate of the extent to which the sizes of consecutive moults of individuals were related. The error variance from the multiple regression was used to estimate the variability in moult increment that was independent of the combined effects of pre-moult CL and consistent differences between individuals.

The variability in moult increment from measurement error was estimated for each group, independently of the multiple-regression analysis, using the variance of the measurement errors that were isolated from the mark-recapture data. Measurement error variance was then expressed as a percentage of the error variance from the multiple regression for each group.

Moult Increment Related to Pre-moult Carapace Length

This relationship was illustrated using final results of the analyses of variation in moult increment with respect to sex, season and location. Regression lines and 95% confidence belts for each of the final sets of seasons for each size class were plotted, together with moult increments of individuals exceeding 70mm CL.

Using the method of Mauchline (1977) moult increment was expressed as a percentage of pre-moult CL, to provide a 'growth factor'. The linear and $\log_{10}$_linear regressions of growth factors on pre-moult CL were then determined. Individuals with moult increments recorded from seasons of maximum growth were allocated to a series of size classes (5mm width), commencing at 19.95mm.

Growth factors were calculated for individuals and linear regressions of growth factor and $\log_{10}$ growth factor on pre-moult CL determined for the whole range of carapace lengths. Correlation coefficients for each relationship were determined and tested for significant departures from zero and each other (Snedecor and Cochran 1967). The same procedure was applied to the combined data for *E. spinifer* over 70mm CL and individuals with increments recorded from seasons of minimum growth.

RESULTS

Annual Moult Frequency

Small individuals (20–35mm CL) were characterised by a moult frequency of three, although a few specimens moulted from one to six times per year. Medium crayfishes (35–55mm CL) typically moulted twice per year, with occasional individuals moulting once or three times; all seven large males and 14 large females recorded had moulted once over 12–15 month periods, another large female moulted twice (see Fig. 1).

All annual frequencies of one were based on actual numbers of moult increments recorded - not on estimates. There were no apparent differences in annual moult frequencies with respect to either sex or location for the small or medium groups. Moult frequencies of large males and females from Pool 3 were similar to each other, and to the single value from Pool 7.
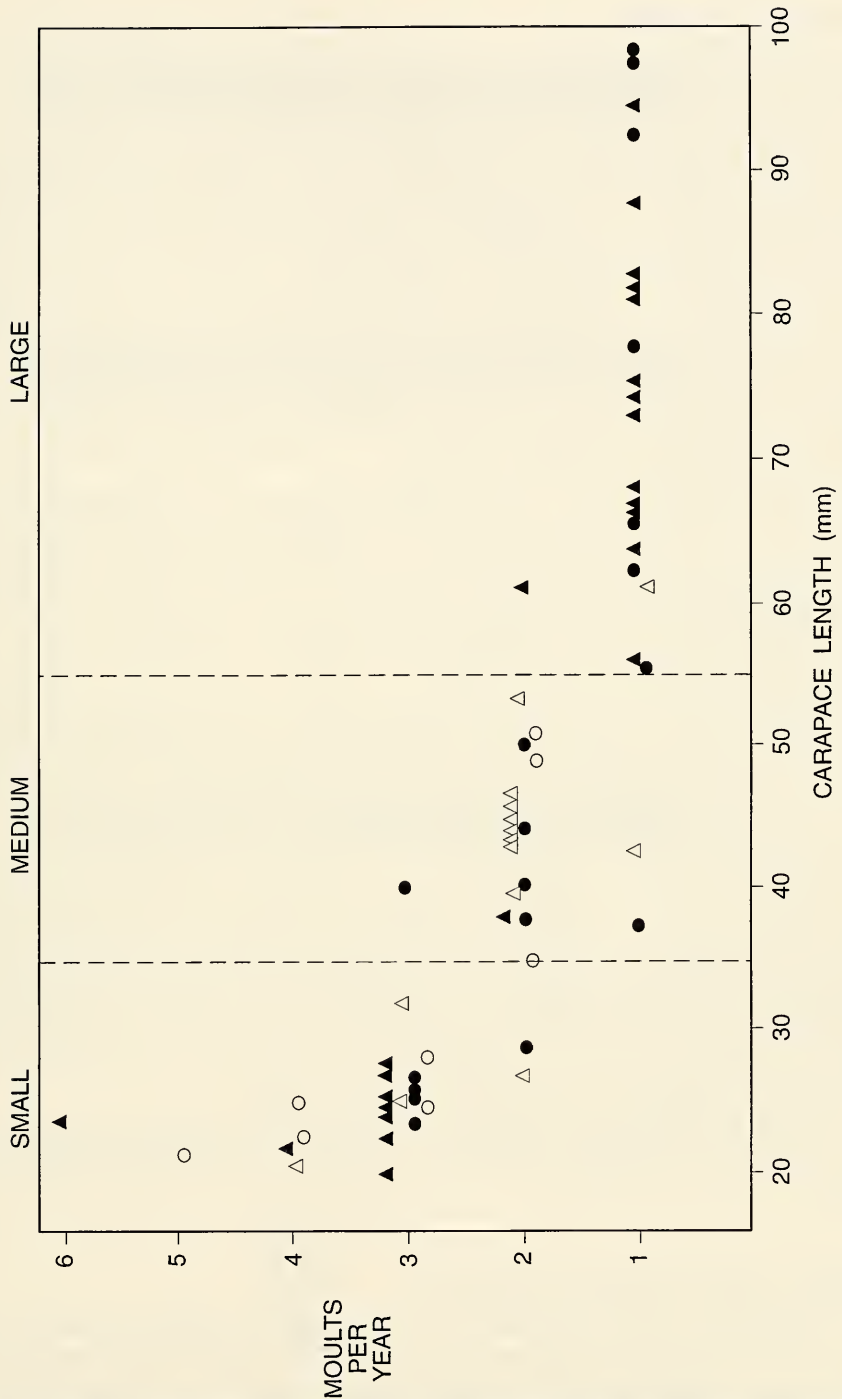
Figure 1. Summary of annual moult frequency related to initial carapace length in *E. spinifer*. Group ranges: small = 20–35mm CL; medium = 35–55mm CL; large = 55–100mm CL. Key to symbols: ○ = Pool 7, male; ● = Pool 3, male; Δ = Pool 7, female; ▲ = Pool 3 female.

Seasonality in Moulting

Trends in percentage of post-moult and non-moulting individuals of small and medium size were similar for males and females in both locations, while trends for large males and females were distinctly different.

Moulting activity among small individuals commenced rapidly during September 1977, decreased rapidly during mid-April to mid-May 1978 and increased rapidly again during October 1978. There was a pronounced decrease in moulting activity in Pool 3 from mid-December 1977 to March 1978, while a less pronounced decrease occurred among small specimens in Pool 7 over the same period.

Two periods of moulting activity per year were evident for medium-sized *E. spinifer* from Pool 3, during the periods October-November 1977 and February-April 1978; moulting activity commenced again during October 1978. Trends for medium-sized specimens in Pool 7 differed in two major respects. Firstly, despite normal sampling, no medium-sized *E. spinifer* were collected from October to December 1977 although this period coincided with a peak of moulting activity in this size class from Pool 3. Secondly, the other major period of moulting in Pool 7 is from March-May 1978 compared with February-April 1978 in Pool 3.

Trends in percentages of large, non-moulting females were similar for both locations. In Pool 7, the increasing percentage of non-moulting individuals, marking the end of the moulting season, occurred in two steps commencing slowly during March-May 1978, followed by a sharp increase in June; while in Pool 3 a single, sharp increase occurred during June 1978. The major peak in post-moult percentage occurred in May 1978 at both sites; by contrast, moulting activity commenced during April in Pool 3 and during February in Pool 7.

Recapture records indicated that the small peaks in percentage of post-moult crays for September 1977 and 1978, in Pool 3, were due to individuals that had not moulted since the previous major peaks of moulting activity. High percentages of both post-moult and non-moulting individuals during May-June 1977 indicated that a period of moulting activity had occurred just prior to this in both pools.

The trends in percentage of large, non-moulting males from the two locations appeared to be of similar configuration; they were also related in the same general manner as those described for females of similar size, although data for Pool 7 were incomplete. Changes over time in percentages of both post-moult and non-moulting males were quite different from those recorded for large females. In Pool 3, the initial increase in percentages of large, non-moulting males indicated the finish of the major period of moulting activity during January 1978; moulting had been initiated during November 1977. Although percentages of large, post-moulting males in Pool 7 were absent for the initial part of this period, values for October 1977 and January 1978 indicated that large males had also moulted in Pool 7 during November-January.

The May 1977 peak in percentage of large, post-moult males in Pool 7 resulted from two specimens (59.4mm, 63.4mm CL); recapture data indicated that both of these individuals had moulted during late 1977 and again during the period January–May 1978.

Moulting Activity and Water Temperature

Variations in water temperature were strongly seasonal; although similar for both pools the 1977–78 summer temperatures for Pool 7 were 2–3°C lower than those for Pool 3 (Fig. 2). Moulting activity of small *E. spinifer* commenced as water temperatures increased to levels substantially greater than 14°C during September 1977 and October 1978, whereas moulting activity ceased as water temperatures decreased below approximately 15°C during May 1978.
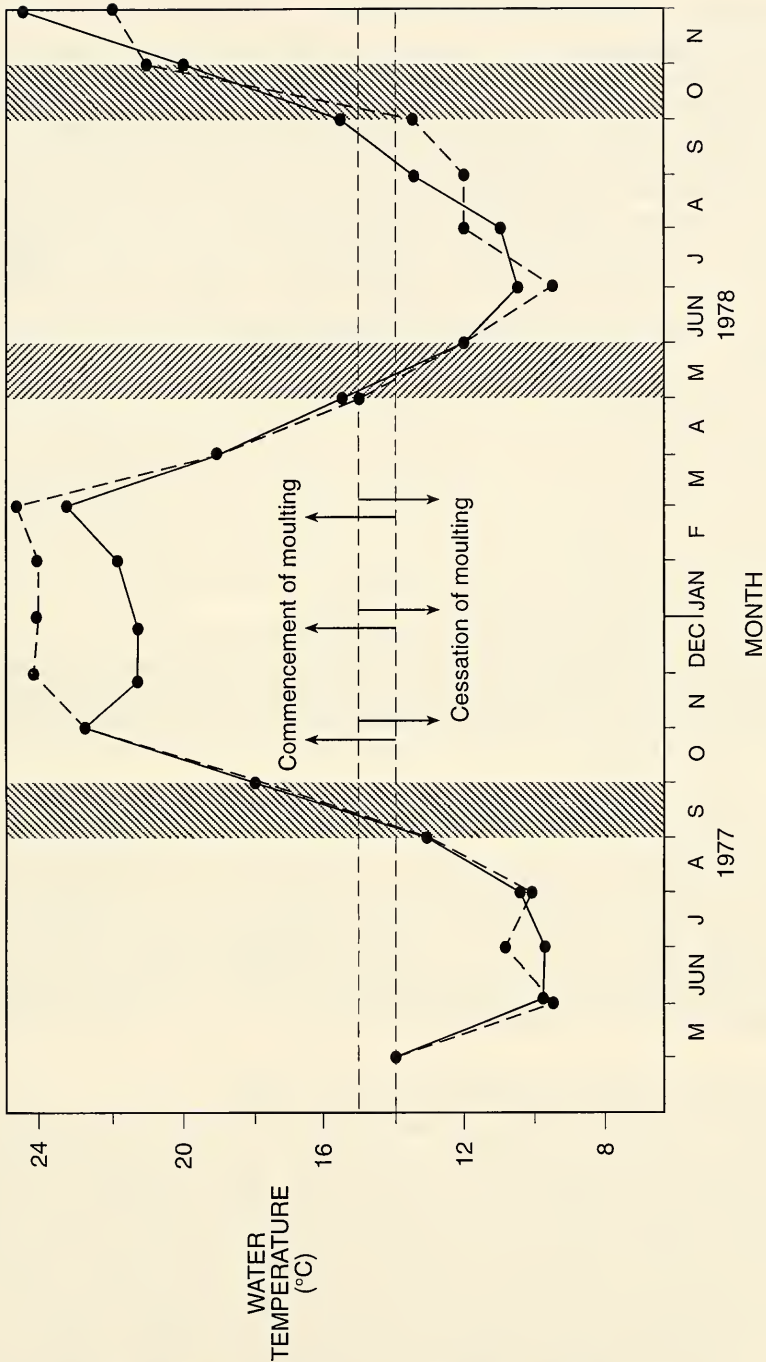
Figure 2. Summary chart of water temperatures in two Loddon River pools and identified moulting activity in small *E. spinifer* (20–35mm CL) over an 18 month period. Key to symbols: — = monthly water temperature for Pool 3; – – = monthly water temperature for Pool 7; ☑ = month for commencement of moulting activity; ◨ = month for cessation of moulting activity.

Moult Increment and Sex, Season or Site

No significant differences were detected between slopes of the regressions of moult increment on pre-moult CL in any of the comparisons for sex, season or location; however, separate regressions (increment on pre-moult CL) for each class at each location for the seasonal periods demonstrated the following. No significant differences were detected among seasons for individuals in Pool 7, but significant differences were present among seasonal regressions for the small class (20–35 mm CL) in Pool 3 (p <0.005). The Student Newman Keuls test indicated that elevations of regressions for May-October 1977 and February-August 1978 were similar (p >0.05), and significantly greater than the elevation of the October 1977– February 1978 regression (p <0.001); for *E. spinifer* of 35–55mm CL in Pool 3, the elevation of the May-November 1977 regression was significantly greater than that of the December 1977– August 1978 regression (p <0.005).

When seasonal regressions (increment on pre-moult CL) are compared between locations, significant differences were detected among elevations for small and medium size classes (p <0.005). For the 20–35mm size class (Fig. 3), the elevations of regressions for all seasons in Pool 7 as well as May-October 1977 and February-August 1978 in Pool 3 were similar (p >0.50), but significantly greater than the elevation of the regression for October 1977–February 1978 in Pool 3 (p <0.001). For the 35–55mm size class (Fig. 4), elevations of regressions for all seasons in Pool 7 and May-November 1977 in Pool 3 were similar (p >0.20); they were also greater than the elevation of the December 1977–August 1978 regression for Pool 3 (p >0.005).

The elevation of the regression of annual moult increment on pre-moult CL for females with carapace lengths of 55–70mm in Pool 7 was significantly greater than that for Pool 3 (Fig. 5, p <0.005). No significant differences were detected among the elevations of the regressions for precocious males, normal males and females with carapace lengths of 20–25mm for October 1977–February 1978 in Pool 3 (p >0.05, Fig. 6).

Moult Increment Variation and Other Factors

The error variance from the multiple regression of moult increment (Y) on pre-moult CL (X_1) and previous increment (X_2) accounted for a uniformly high proportion of the total variance in moult increment for the different groups of *E. spinifer* (Table 1), with values ranging from 64 to 92%. A large proportion of increment variability was thus independent of both pre-moult CL and consistent differences between moult increments of different individuals. Only a small percentage (3–7%) of this independent variability could be accounted for by increment measurement errors.

Moult Increment Related to Pre-moult Carapace Length

Moult increments of individuals with carapace lengths 20–55mm increased with increasing pre-moult CL at a relatively constant rate for seasons of both maximum and minimum growth at moulting (Fig. 7). Increments of larger specimens (55–70mm CL) were approximately constant with respect to pre-moult length in both locations, although 95% confidence belts for the regression slopes were wide. Data were available for two males and an immature female in the 70–95mm CL range, all from Pool 3; increments of these individuals were close to the average moult increment for the 55–70mm class from the same location. Moult increments of mature females were substantially smaller than those of the two males and immature female of similar size; furthermore, increments of both sexes decreased markedly at a pre-moult CL of approximately 95mm (Fig. 7).

Correlation coefficients of the regressions of both growth factor and $\log_{10}$ growth factor on pre-moult CL were not significantly different from zero (p >0.9) for individuals
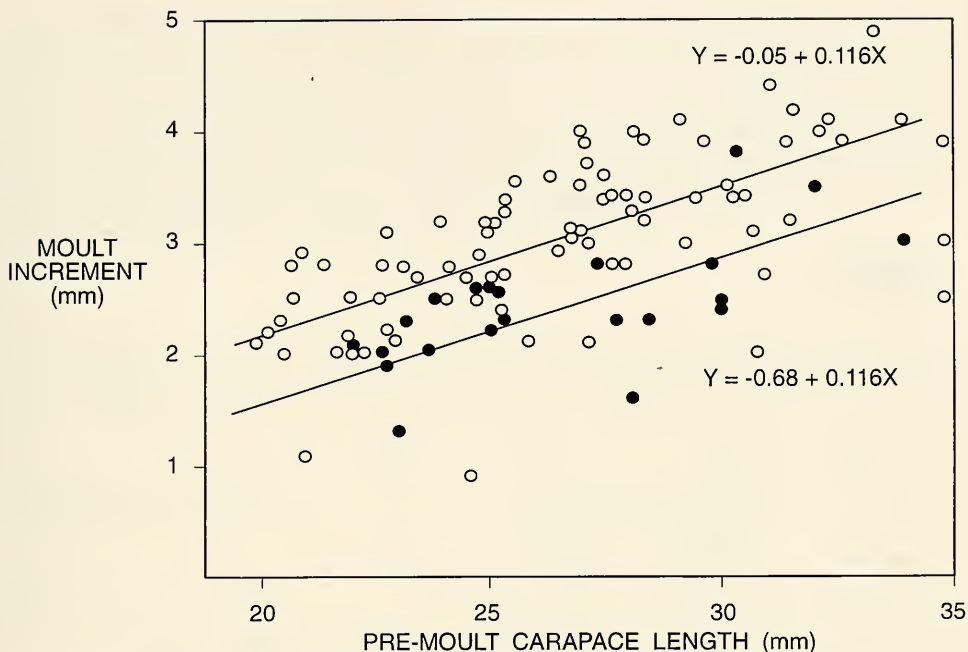
Figure 3. Regressions of moult increment on pre-moult carapace length for small *E. spinifer* (20–35mm CL). Key to symbols: ○ = Pool 3, May–October 1977, February–August 1978 and Pool 7, May–October 1977 and October 1977–February 1978 and February–August 1978 and May–October 1978; ● = Pool 3, October 1997–February 1978.
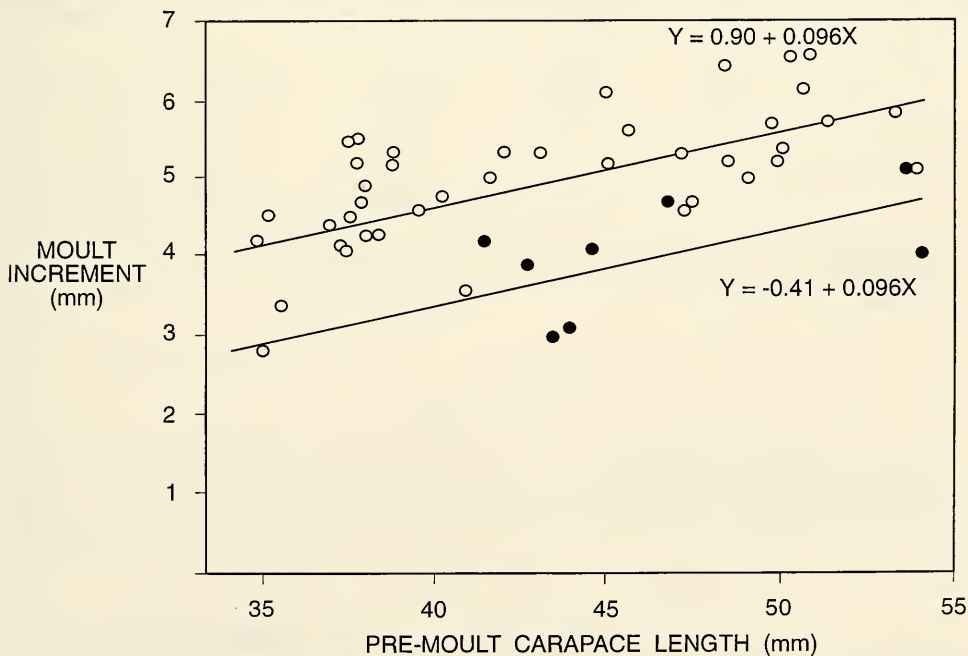

Figure 4. Regressions of moult increment on pre-moult carapace length for medium *E. spinifer* (35–55mm CL). Key to symbols: ○ = Pool 3, May–November 1977 and Pool 7, May–November 1977 and December 1977–August 1978 and May–November 1978; ● = Pool 3, December 1977–August 1978.
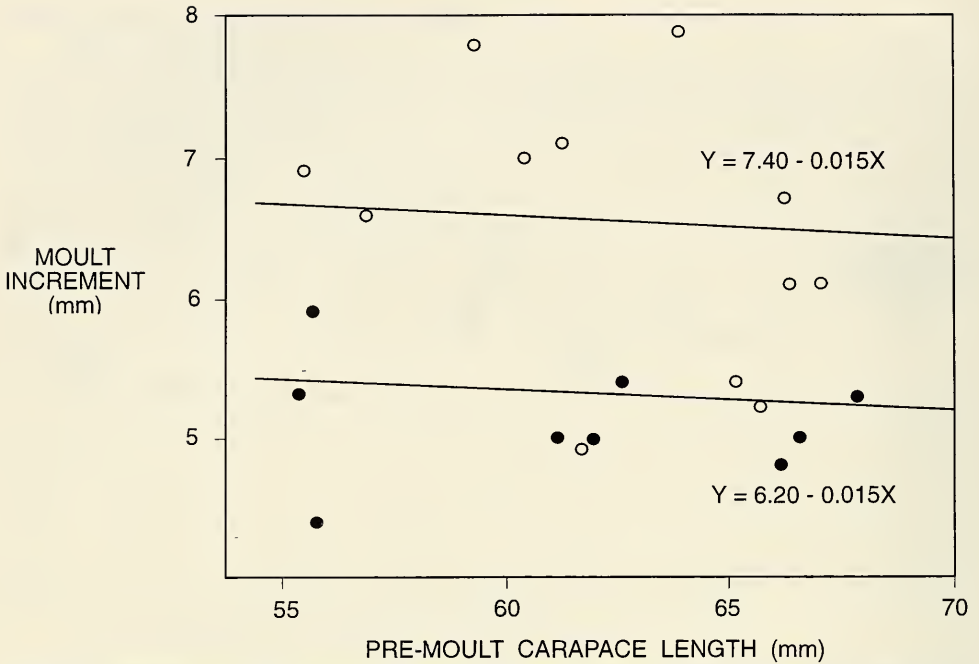
Figure 5. Regressions of moult increment on pre-moult carapace length for large *E. spinifer* (55–70mm CL). Key to symbols: ○ = Pool 7, annual moult increment; ● = Pool 3, annual moult increment.

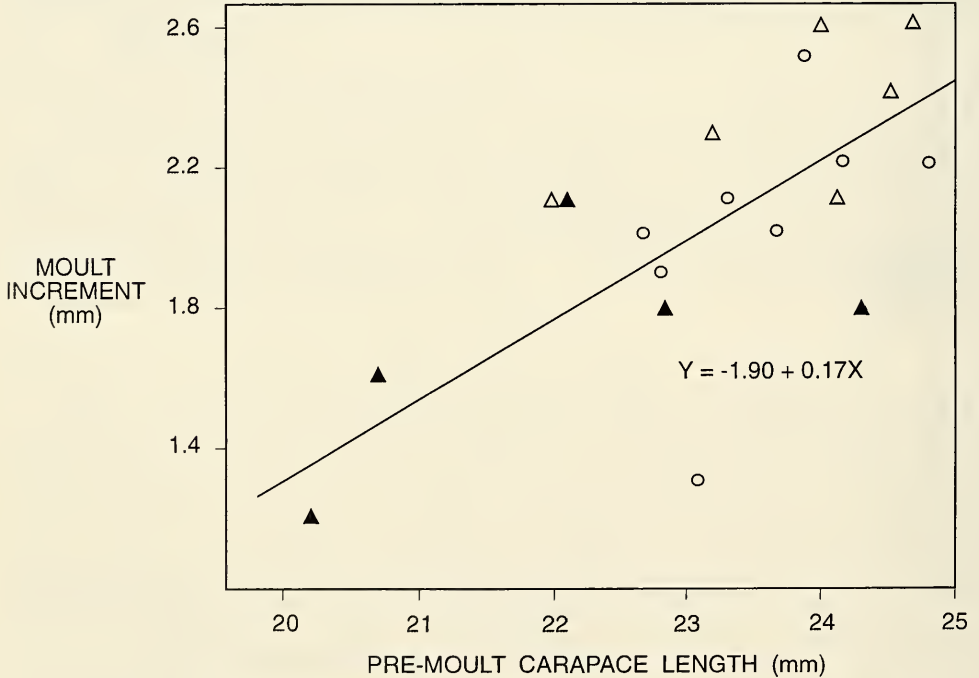*Figure 6.* Overall regression of moult increment on pre-moult carapace length for precocious males, normal males and immature female *E. spinifer* (20–25mm CL) from Pool 3 during the period October 1977– February 1978. Key to symbols: ○ = immature female; Δ = normal male; ▲ = precocious male.

that had moulted during seasons of maximum growth at moulting (Fig. 8). Percent increase in carapace length at moulting was thus approximately constant, with respect to pre-moult CL for these crays, at an average value of about 11.5%. The co-efficients derived for stocks that had moulted during seasons of minimum growth at moulting (Fig. 9) were significantly different from zero (p <0.001), but not from each other (p >0.6). Thus there was a significant decrease in growth factors with increasing CL and the linear and log-linear regressions were of equally good fit; although neither curve provided an adequate fit to the growth factors of the largest individuals.

TABLE 1

Contributions of measurement error and unidentified factors to variation in *E. spinifer* moult increment, based on multiple regressions of moult increment (Y) on pre-moult carapace length (X_1) and previous increment (X_2).

		Site			
		Pool 3	Pool 3	Pool 3	Pool 7
Source of Regression	Size Class (mm)	20–35	20–35	35–55	35–55
	Y Season	Oct 1977–Feb 1978	Feb–Aug 1978	Dec 1977–Aug 1978	Dec 1977–Aug 1978
	X_2 Season	May–Oct 1977	Oct 1977–Feb 1978	May–Nov 1977	May–Nov 1977
	Total (T)*	0.46(9)	0.30(20)	0.63(8)	0.56(7)
Estimates of Variability	Error (E)†	0.32(7)	0.20(18)	0.56(6)	0.52(5)
	%E/T	69	64	89	92
	Measurement (M) ▲	0.010 (66)	0.010 (66)	0.038 (179)	0.019 (92)
	% M/E	3.1	5.1	6.8	3.6

* Total (T) variance in moult increment, with degrees of freedom (d.f.).

† Error (E) variance from the multiple regression of Y on X_1 and X_2, with degrees of freedom (d.f.).

▲ Measurement (M) error variance in Y, estimated from independent data, with degrees of freedom (d.f.).

DISCUSSION

Low catchabilities of very small *E. spinifer* (Turvey and Merrick 1997b) resulted in few data for individuals less than 20mm CL, so descriptions of moulting frequency and increment were confined to individuals above this size. Data were insufficient for the description of moult frequencies of precocious males, although some information on increment size is provided.

Annual Moult Frequency

Direct interpretation from Figure 1 is necessary as data are inadequate for further statistical evaluation. The data indicate that annual moult frequencies are similar for males and females of the same size; this suggestion is supported, for small and medium
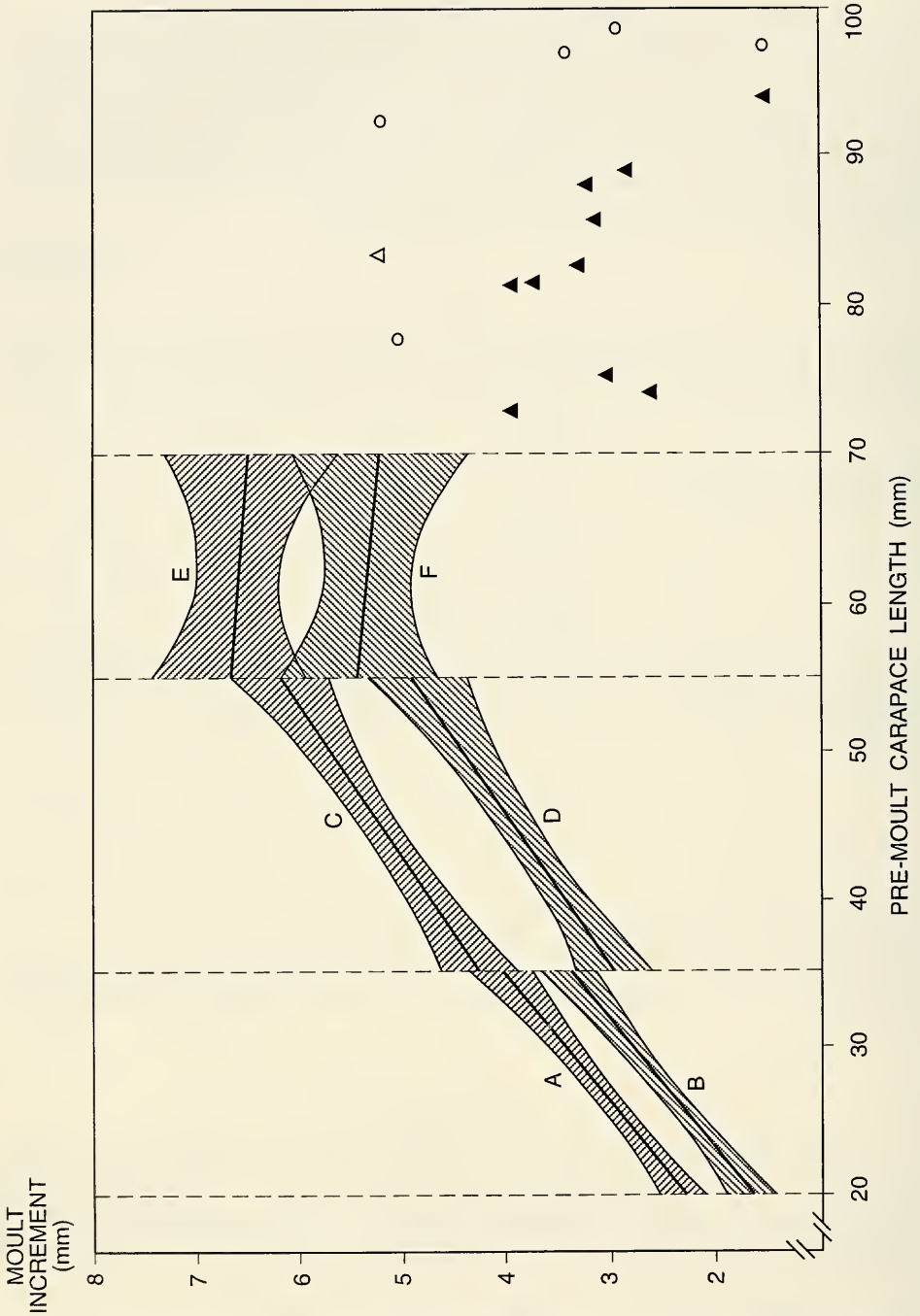
Figure 7. Variation in moult increment with pre-moult carapace length for all *E. spinifer*. Seasons of maximum growth at moulting: A = Pool 7, all seasons and Pool 3, May–November 1977 and December 1977–August 1978; C = Pool 7, all seasons and Pool 3, May–November 1977; E = Pool 7, annual moult. Seasons of minimum growth at moulting: B = Pool 3, October 1977–February 1978; D = Pool 3, December 1977–August 1978; F = Pool 3, annual moult. Key to symbols: O = male, Pool 3, annual moult; Δ = immature female, Pool 3, annual moult; ▲ = mature female, Pool 3, annual moult.
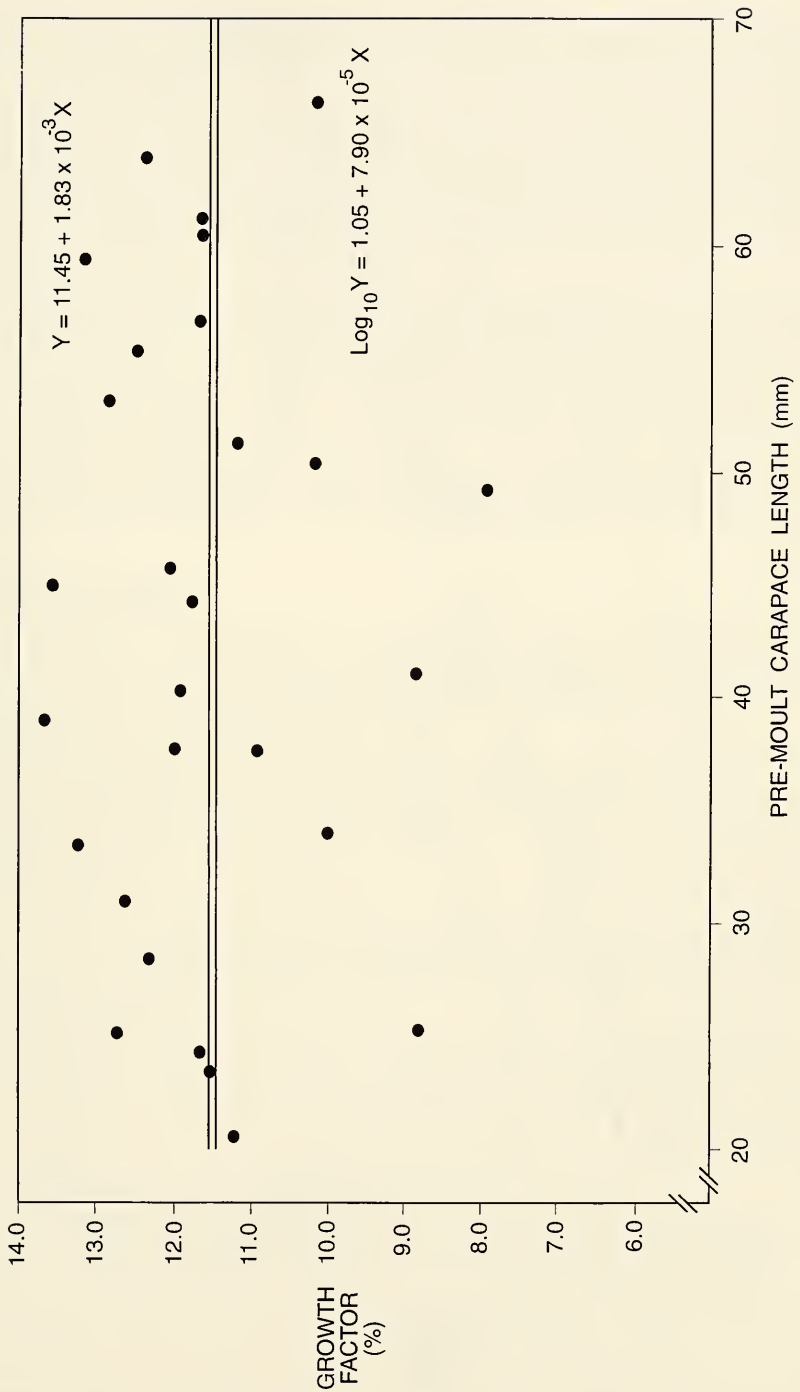
Figure 8. Variation in growth factor with pre-moult carapace length, for male and immature female *E. spinifer* of 20–70mm CL, during seasons of maximum growth at moulting in Pools 3 and 7.
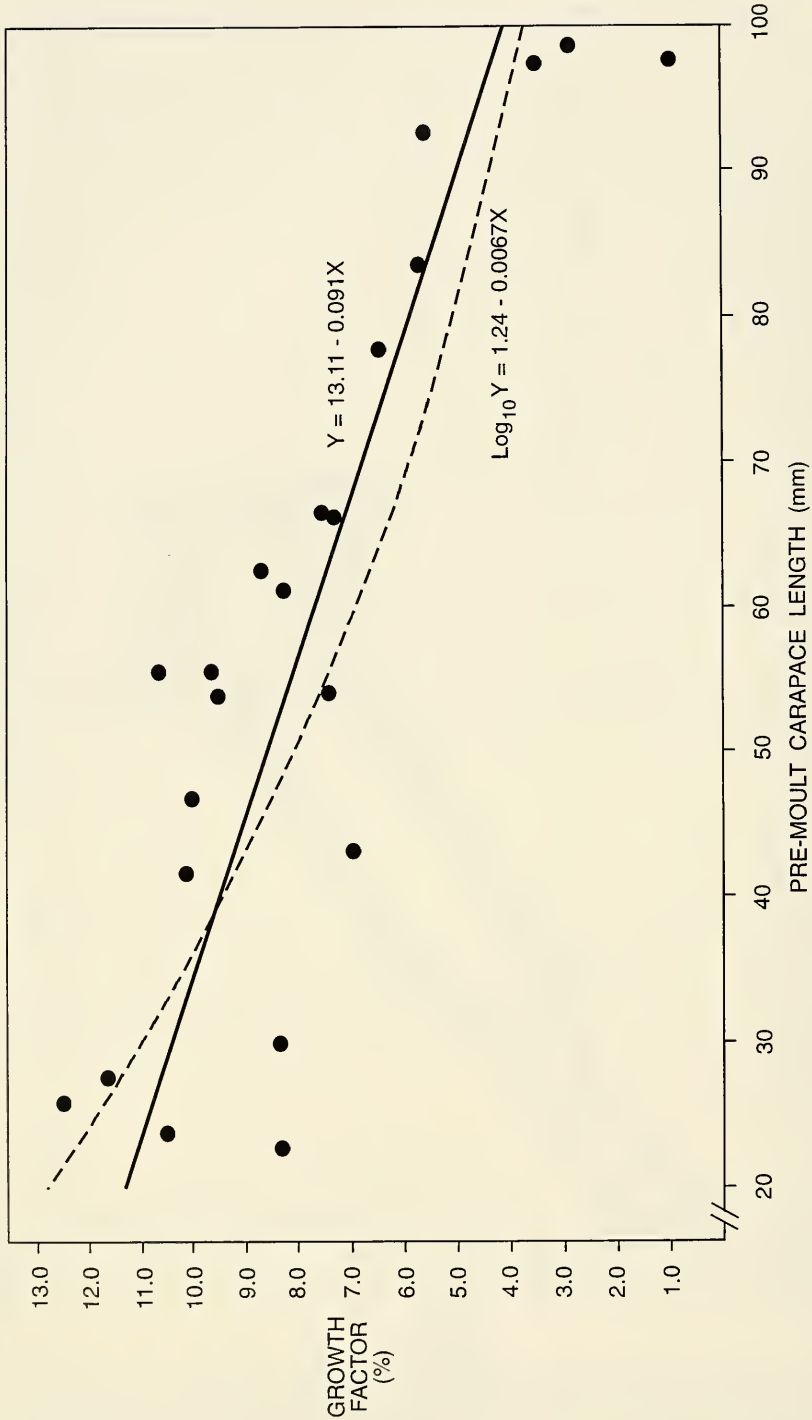
Figure 9. Variation in growth factor with pre-moult carapace length, for male and immature female *E. spinifer* of 20–100mm CL, during seasons of minimum growth at moulting in Pool 3.

classes, by the closeness of seasonal patterns of moulting activity of both sexes. It is also unlikely that there are major differences between moult frequencies of large (>55mm CL) individuals. As 21 out of 22 large specimens moulted once, a single annual moult is probably typical of both sexes.

As normal male *E. spinifer* mature over 45–55mm CL and females at carapace lengths exceeding 70mm (Turvey and Merrick 1997a), annual moult frequencies appear independent of sex and state of maturity. Similarly, Honan and Mitchell (1995) found that growth rates of males and females were not significantly different; they also concluded that *E. bispinosus* up to 50mm CL moulted twice a year, above that size moults became annual.

Although moult frequency in *E. spinifer* is probably independent of sex or maturity, there is clearly a relationship with carapace length. Decreases in frequency with increasing size have been recorded for many large decapods (Kurata 1962). Records for some lobster and crab species (Bennett 1974; Cooper and Uzmann 1971) indicate that this decrease may be continuous over the whole size range of a species, resulting in frequencies of less than one per year in mature individuals. This is not the case for *E. spinifer,* where moulting occurs at a constant frequency of once a year over much of the upper part of the size range. Similar results have been obtained for species in two other parastacid genera (Hopkins 1967a; Shipway 1951; Sokol 1988).

Seasonality in Moulting

Seasonal patterns of moulting activity differ for small, medium and large *E. spinifer* in accordance with differences in annual moult frequency. A different method had to be used to measure decreasing moulting activity because individuals could remain in moult stage Ce for several months after moulting.

Small individuals typically moult three times each year, sometimes more; moulting activity in the field population is continuous, with fluctuations in intensity from early spring to late autumn. The majority of the medium class moult twice a year and moulting activity is largely confined to two discrete periods, one in spring and one in autumn. The annual moult in large individuals is usually confined to a single relatively brief period, early summer for males or late autumn for females. By comparison, Honan and Mitchell (1995) were unable to precisely determine a moulting season for adult *E. bispinosus.* They showed that: *E. bispinosus* moulted between late spring and late autumn; juveniles moulted 11–12 times in their first year to reach ~20mm CL; small individuals (20–30mm CL) moulted 3–4 times in the second year; above this sub-adults typically moulted twice per year until ~50mm CL.

The above generalisations relating to *E. spinifer* were based on the allocation of individuals to arbitrary discrete size classes for the purposes of analysis. In the field average moult frequencies and hence seasonal patterns of moulting activity, probably changed continuously with carapace length until the adoption of a single annual moult. A number of departures from the suggested generalised pattern are possible, including some individuals moulting twice annually when just above 55mm CL.

The different moulting seasons of large males and females contrasted with the simultaneous seasons of smaller individuals and with annual frequencies of the rest of the population. In other crays, males moult at various times, but females typically moult just after the release of juveniles or just before mating (Hopkins 1967a,b; Payne 1972; Weagle and Ozburn 1972). In mature *E. spinifer* females moulting occurred prior to mating in May, rather than after the release of juveniles in December. This proximity of moulting to mating and oviposition may be related to the need for pleopodal setae to be in good condition for egg attachment. But other influences on moult timing would include the long incubation period (precluding moulting) and the need to accumulate large reserves of nutrients for egg production.

Moulting Activity and Water Temperature

The comparison of moulting activity and water temperature was confined to the small class, as they moulted more frequently and changes in patterns of moulting activity provided a more sensitive indication of altered metabolic responses to environmental parameters. Results suggested an association between growth processes and water temperatures, with growth being initiated above 14–15°C. This conclusion contrasts with findings of studies on some North American crayfishes showing that growth is regulated by photoperiod (Aiken 1969; Armitage et al. 1973); although increased moult frequency with increasing temperature has been reported for a number of European and Australasian species (Hopkins 1967a; Lowery 1988). Hopkins (1967a) found that while frequencies decreased during winter for the New Zealand parastacid, *Paranephrops planifrous*, moulting activity did not cease. This suggests a lowering of moulting activity, rather than an absolute threshold below which growth cannot occur. This may also apply to *E. spinifer*, since at least two individuals moulted outside the normal season, with ambient temperatures well below 14°C.

Moult Increment and Sex, Season or Site

There were no significant differences between the moult increments of immature female and normal male *E. spinifer* up to 70mm CL; the increments recorded for the two males and immature female in the 70–95mm CL range were similar in size. In the one instance where data were adequate for testing, there were no significant differences among the moult increments of precocious males, normal males or immature females that could not be accounted for by CL differences.

While there is general similarity between the increments of males (regardless of maturity) and immature females, the increments of mature females are smaller than those of the two males and immature female of comparable size. It is suggested that, for *E. spinifer*, reproduction acts to decrease the size of moult increments in females but not in males; this effect has been recorded in other large crayfishes (Hopkins 1967a; Lowery 1988; Sokol 1988).

Moult Increment Variation and Other Factors

Considerable variation in increments was also present, in all groups of *E. spinifer*, independent of the trends described above. The multiple regression analysis indicated that most of this variability could not be attributed to effects of pre-moult CL or other genetically based differences between individuals. Up to 7% of this independent variation could be attributed to errors in increment measurement; but measurement errors in pre-moult CL and previous increment could only have contributed a proportion of the remaining variation. Some 50–80% of total variability cannot be explained and potential causes of this variation are discussed below.

Firstly, variation in increment has been linked with food availability in *Cherax destructor* (Sokol 1988) and some indirect evidence of fluctuating feeding success has been presented for *E. spinifer* (Turvey and Merrick 1997c). As the major component of the *E. spinifer* diet is decaying plant material of terrestrial origin (Turvey and Merrick 1997c) an erratic supply may have contributed to the observed situation. Substantial input of this allochthonous material only occurred during flooding events, which happened two or three times per year at irregular intervals. Furthermore, once debris entered the water-course it was distributed unevenly in small isolated deposits. Secondly, moult increments in other parastacids are known to be affected by population density (Morrissy 1975; Sokol 1988); however, in the absence of data on the carrying capacity of the Loddon River habitat or *E. spinifer* population numbers no further comment is possible.

Moult Increment Related to Pre-moult Carapace Length

Growth factors (increments expressed as a percentage of pre-moult CL) ranged from 14% in juveniles to 6–1% for large adult *E. spinifer*, covering a range similar to those recorded for two other parastacids (Hopkins 1967a; Shipway 1951).

Although absolute values of average increments of *E. spinifer* varied with both season and location, the slopes of the relationships between increment and pre-moult CL within a size class were unaffected by such variation (Fig. 7). Hence changes in the slopes of these relationships are likely to be fundamental to the patterns of growth of *E. spinifer* in the area, rather than effects of variable external factors. The change from an increase in moult increment with pre-moult CL for the 20–55mm group to a constant increment for individuals of 55–70mm CL is considered to be both real and general; although confidence limits for the slopes of the latter regressions were wide (Fig. 7). As moult frequency dropped from typically twice to once per year at approximately 55mm CL, there is an association between the onset of a constant moult increment and the adoption of a single moult per year.

Kurata (1962) found that Hiatt growth diagrams of numerous crustaceans were characterised by abrupt changes in slope, which he termed 'inflexions'; these inflexions were frequently independent of gonad maturation. Similar relationships have now been documented for lobsters, cambarid crayfishes and other parastacids (Farmer 1973; Jones 1981; Newman and Pollock 1974; Payne 1972; Weagle and Ozburn 1972). The relationship between increment and pre-moult CL for *E. spinifer* appears to conform to a general decapod growth pattern, with an increase in increment with body size followed by a constant or decreasing moult increment.

On the other hand, the equations relating growth factors and pre-moult CL proposed for decapods by Mauchline (1977) do not closely describe the relationship in *E. spinifer* (Figs. 8 and 9), for moults undergone during similar growing seasons. But this does not imply that *E. spinifer* differs fundamentally from other decapod taxa in its growth patterns. Rather, it suggests that the equations do not adequately describe the relationship between growth at moulting and size over the greater part of the growth history of the species.

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